

Behaviour and Conservation

Edited by

L. MORRIS GOSLING

University of Newcastle upon Tyne

AND WILLIAM J. SUTHERLAND

University of East Anglia



CAMBRIDGE
UNIVERSITY PRESS



THE ZOOLOGICAL
SOCIETY OF LONDON

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS

The Edinburgh Building, Cambridge CB2 2RU, UK <http://www.cup.cam.ac.uk>

40 West 20th Street, New York, NY 10011-4211, USA <http://www.cup.org>

10 Stamford Road, Oakleigh, Melbourne 3166, Australia

Rue de Alarcón 13, 28014 Madrid, Spain

© The Zoological Society of London 2000

This book is in copyright. Subject to statutory exception
and to the provisions of relevant collective licensing agreements,
no reproduction of any part may take place without
the written permission of Cambridge University Press.

First published 2000

Printed in the United Kingdom at the University Press, Cambridge

Typeset in FFScala 9.75/13 pt [VN]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

Behaviour and conservation / edited by L. Morris Gosling and William J. Sutherland.
p. cm.

Includes bibliographical references (p.).

ISBN 0 521 66230 3 (hbk). – ISBN 0 521 66539 6 (pbk.)

1. Conservation biology. 2. Animal behaviour. I. Gosling, L.
Morris, 1943–. II. Sutherland, William J.

QH75.B45 2000

333.95'16–dc21 99-26461 CIP

ISBN 0 521 66230 3 hardback

ISBN 0 521 66539 6 paperback

Contents

List of contributors [ix]

Part I Introduction

- 1 Advances in the study of behaviour and their role in conservation [3]

WILLIAM J. SUTHERLAND & L. MORRIS GOSLING

Part II Conservation impact of people

- 2 The evolutionary ecology of human population growth [13]

RUTH MACE

- 3 Grassland conservation and the pastoralist commons [34]

MONIQUE BORGERHOFF MULDER & LORE M. RUTTAN

- 4 Predicting the consequences of human disturbance from behavioural decisions [51]

JENNIFER A. GILL & WILLIAM J. SUTHERLAND

- 5 The role of behavioural models in predicting the ecological impact of harvesting [65]

JOHN D. GOSS-CUSTARD, RICHARD A. STILLMAN

ANDREW D. WEST, SELWYN MCGRORTY,

SARAH E.A. LE V.DIT DURELL & RICHARD W.G. CALDOW

Part III Habitat loss and fragmentation

- 6 Butterfly movement and conservation in patchy landscapes [85]

CHRIS D. THOMAS, MICHEL BAGUETTE & OWEN T. LEWIS

- 7 Life history characteristics and the conservation of migratory shorebirds [105]

THEUNIS PIERSMA & ALLAN J. BAKER

- 8 Ranging behaviour and vulnerability to extinction in carnivores [125]

ROSIE WOODROFFE & JOSHUA R. GINSBERG

- 9 Habitat fragmentation and swarm raiding army ants [141]
GRAEME P. BOSWELL, NIGEL R. FRANKS
& NICHOLAS F. BRITTON

Part IV Sexual selection, threats and population viability

- 10 Sexual selection and conservation [161]
ANDERS PAPE MØLLER
- 11 Dispersal patterns, social organization and population
viability [172]
SARAH DURANT
- 12 Incorporating behaviour in predictive models for
conservation [198]
RICHARD A. PETTIFOR, KEN J. NORRIS
& J. MARCUS ROWCLIFFE
- 13 Controversy over behaviour and genetics in cheetah
conservation [221]
TIM CARO
- 14 The role of animal behaviour in marine conservation [238]
JOHN D. REYNOLDS & SIMON JENNINGS

Part V Conservation applications of behaviour

- 15 Communication behaviour and conservation [261]
PETER K. MCGREGOR, THOMAS M. PEAKE
& GILLIAN GILBERT
- 16 Reducing predation through conditioned taste aversion [281]
DAVID P. COWAN, JONATHON C. REYNOLDS
& ELAINE L. GILL
- 17 Retaining natural behaviour in captivity for re-introduction
programmes [300]
MICHAEL P. WALLACE
- 18 Consequences of social perturbation for wildlife management and
conservation [315]
FRANK A.M. TUYTTENS & DAVID W. MACDONALD
- 19 Animal welfare and wildlife conservation [330]
ELIZABETH L. BRADSHAW & PATRICK BATESON

References [349]

Index [418]

Advances in the study of behaviour and their role in conservation

WILLIAM J. SUTHERLAND & L. MORRIS GOSLING

The merging of evolutionary theory and classical ethology produced the field of behavioural ecology, which has flourished over the last 25 years. At the same time, conservation biology has emerged as a loosely knit, but thriving, group of the disciplines that aim to support the conservation of biodiversity. Behavioural ecology has remained principally an area of fundamental research while conservation biology is shaped by increasing concern about accelerating threats to biodiversity and is thus essentially strategic in character. Despite obvious areas of common interest, there has been surprisingly little mixing of behavioural and conservation biology. Most important, there has been very little benefit for conservation from the major advances in the understanding of wild animals that behavioural ecology has produced.

Many conservation projects do in fact include aspects of animal behaviour but usually only in a trivial way. For example, many determine the home range or diet of a species of conservation concern. Typically, these treatments do not refer to the body of theory that is now available and, partly because of this, they are rarely used predictively.

The lack of contact between these areas of theory and application is particularly surprising because many behavioural ecologists have a personal commitment to conservation. A number of field ethologists are deeply involved in conserving their study species and usually to a degree that goes well beyond the selfish motive of ensuring that a population persists until the study is completed. Indeed, some of the sites that are best protected from poaching are those used for behavioural research.

Why then do so few ethologists apply their behavioural skills to answer conservation questions? Or, more generally, why has behavioural ecology not been incorporated into conservation biology, the body of strategic re-

search that is most commonly used to address practical conservation questions? We can think of five main reasons and suspect that all of these sometimes play a role: (1) conservation biology and conservation are not perceived as rigorous subjects and thus are not considered prestigious; (2) there is a cultural separation between behavioural ecology and conservation: most behavioural ecologists work in universities and, because they may not regularly meet practising conservationists who tend to work for state organizations or charities, they have few opportunities to experience real conservation issues; (3) patterns of funding tend to follow and reinforce these cultural divisions: for example, the British Research Councils tend to fund basic research while most funding for conservation projects comes from trusts and charities; (4) there may simply be a historical lag: both behavioural ecology and conservation biology are young disciplines and there is little tradition of combining the two; (5) it is sometimes technically difficult to combine the two subjects. For example, to achieve conservation objectives the role of behaviour is often expressed through population processes and many ethologists may have little expertise in population ecology.

We believe that studies of behaviour and conservation have a great deal to offer each other. This cross-play can happen at a number of levels. For example, the high priority given to conservation helps provide a justification for theoretically based studies of behaviour and this may become increasingly important to justify research spending. Studies of behaviour can also provide essential new insight into intractable conservation problems. Perhaps most important, it can also be argued that an evolutionary understanding of the behaviour of individuals in populations allows us to predict responses under changed conditions with greater confidence than in the case of higher-level processes.

When inviting contributions to this book, we tried to select major developments in behavioural ecology that had important relevance to conservation. These areas are listed in Table 1.1. The table also shows how the chapters relate to the behavioural concepts and their application.

Behavioural ecology and conservation biology have developed largely independently over the last quarter century. Thus, it is surprising that, as shown by the chapters in this book, so many fruitful links have been established between the two fields in the last few years. However, inevitably the occurrence of such links is patchy and there are a number of areas that have rich potential for interesting behavioural research and considerable implications for conservation. We will enlarge on three of these: culture, sensory inputs and the source and consequences of individual behaviour.

Understanding how natural selection and evolution operate provided the key that enabled behavioural ecology to flourish. The understanding of cultural evolution is much less advanced, although there is a theoretical framework for understanding how ideas mutate, are transmitted and are selected for or against (Dawkins, 1976; Cavalli-Sforza & Feldman, 1981; Boyd & Richardson, 1985). We believe that this is a much neglected research area in behaviour. Understanding how culture is transmitted is likely to aid the re-introduction of captive-bred animals (Sutherland, 1998). Many re-introduction attempts have failed because captive bred animals often lack basic survival skills such as the ability to negotiate complex vegetation, recognize and respond to predators, distinguish toxic from palatable food, breed successfully or locate water (Myers *et al.*, 1988; Price, 1989; Beck *et al.*, 1994). Other animals are reintroduced relatively easily after quite simple pre-release procedures (for example, Arabian oryx, *Oryx leucoryx*, Stanley Price, 1989) but we cannot yet predict this variation. Other effects of captivity, such as the ability of animals deprived of extensive social groups for generations to compete for and choose mates, have not been investigated, nor monitored in released populations. Understanding culture transmission will also be essential where it is needed to manipulate the behaviour of animals in protected areas and other sorts of fragmented habitats to help ensure their survival in a changed world. Examples are pioneering attempts to change nesting locations or migration routes (Essen, 1991) to help conserve threatened populations.

There has been relatively little work on the behavioural consequences of the way in which animals sense their environment. Such work will involve the collaboration of physiologists and behavioural ecologists and seems likely to be an exciting research area (Wehner, 1997). Practising conservationists have tricks for encouraging captive and wild animals to breed, care for young, eat novel foods or recognize and avoid predators. However major problems remain, such as behavioural incompatibility in captive-breeding programmes where animals selected for breeding fail to breed; valuable and rare animals, such as clouded leopards, *Neofelis nebulosa*, sometimes fight and may be injured or killed. Two areas of behavioural research have the potential to overcome such problems. The first is the expanding area of signalling theory which promises to provide important generalizations about the way that animals transmit information, and particularly about honest signals of competitive ability and mate quality. Second, it seems likely that detailed understanding of the mechanisms by which animals acquire sensory information may greatly improve the sophistication of

Table 1.1
Developments in behavioural ecology and their implications for conservation

Subject	Consequences for conservation (examples)	Author (chapter number)
Mating systems and sperm competition	Determines effective population size and thus viability	Durant (11)
Sexual selection and status signalling	Costs of display structures reduce mean fitness and thus increase extinction probability	Møller (10)
Sociality and kin selection	Consequences for population ecology and extinction probability	Pettifor <i>et al.</i> (12); Boswell <i>et al.</i> (9)
Life histories	Life-history characteristics and behavioural responses allow an understanding of responses to exploitation	Reynolds & Jennings (14)
	Modelling human reproductive decisions allows realistic prediction of demographic changes	Mace (2)
Evolutionary stable strategies	Can be used to predict density dependence, and thus population size, and the consequences of environmental change	Goss-Custard <i>et al.</i> (5); Gill & Sutherland (4); Pettifor <i>et al.</i> (12)
Social constraints on human resource exploitation	Predicting human impact on habitats and threatened species	Mace (2);
Cultural evolution/learning	Pre-release training and behavioural manipulation during re-introduction schemes	Borgerhoff Mulder & Rutten (3) Wallace (17)
	Using conditioned taste aversions to protect threatened species from predators	Cowan <i>et al.</i> (16)

Communication	Using calling to improve population censuses	McGregor <i>et al.</i> (15)
	Failure to communicate may accelerate population declines	McGregor <i>et al.</i> (15)
Migration	Trading-off fat storage against other physiological requirements	Piersma & Baker (7)
	Design of protected areas and predicting local extinction as a result of hunting along edges	Woodruffe & Ginsberg (8) Thomas <i>et al.</i> (6)
	Dispersal can be manipulated to retain individuals that would otherwise leave the area	Thomas <i>et al.</i> (6)
	Reserve shape and habitat structure influence dispersal and the probability of local extinction	Boswell <i>et al.</i> (9)
Foraging behaviour	Understanding habitat choice	Pettifor <i>et al.</i> (12)
Predation and anti-predator behaviour	Predation as a population limiting factor	Caro (13)
	Designing refuges for threatened prey species	Caro (13)
	Using the normal anti-predator behaviour of a species to understand its responses to hunting	Bradshaw & Bateson (19)
Responses to disturbance	Population consequences of disturbance by people	Gill & Sutherland (4)
	Social disruption may lead to increased levels of disease transmission	Tuytens & Macdonald (18)
	Assessing levels of stress and welfare standards in conservation management and exploitation schemes	Bradshaw & Bateson (19)

captive-breeding techniques. For example, it is now appreciated that the perception of ultraviolet light may be important in determining mate choice in birds (Bennett *et al.*, 1996). Signalling theory and understanding of mechanism will help us to (1) provide the conditions needed for natural patterns of mate choice (for example, glass or plastic screens may reduce ultra violet light and affect mate choice) or (2) manipulate behaviour to achieve practical goals, such as encouraging mating with an animal of low attractiveness (which might otherwise be rejected) to maximize outbreeding in captive-breeding programmes.

Variation in the behaviour of individuals is crucial in explaining demographic processes, such as density dependence, because these are determined by the extent to which density affects the chance of survival or breeding of different individuals (e.g. Sutherland, 1998). For example, individuals may vary in competitive ability and thus in the interference they experience. They may thus differ in the extent to which intake rate declines with density. Individuals may also vary in foraging efficiency or in the intake necessary for survival. Such variation will largely determine which and how many individuals starve at different population levels (Sutherland & Dolman, 1994) and may be related to genotype, environment, parasite load and life history. Understanding the origin and persistence of this variation is thus of fundamental importance in studies of behaviour, in population biology and in practical conservation.

Although the idea of linking behaviour and conservation is very recent, there has been a flurry of interest (Ulfstrand, 1996; Clemmons & Bucholz, 1997; Caro, 1999). The level of enthusiasm was shown by the fact that the joint meeting of the Association for the Study of Animal Behaviour and The Zoological Society of London on which this book was based was one of the best attended of either society. As with most young subjects there is not yet a coherent set of concepts or a core of theory. However, it is pleasing to note a number of repeated themes throughout the book. For example, Woodroffe & Ginsberg (Chapter 8) show that human persecution along the edges of protected areas can explain much of the likelihood of extinction. Thomas *et al.* (Chapter 6) show that butterflies may also be lost from the edge of habitat blocks by the simple mechanism of wandering off-site. In both cases, critical reserve area can be linked to home range although for the silver-studded blue, *Plebejus argus*, the area is 0.0005 km² while for the African wild dog, *Lycaon pictus*, it is 3606 km²!

ACKNOWLEDGEMENTS

We thank The Zoological Society of London and the Association for the Study of Animal Behaviour for funding the conference that provided a starting point for this book. We are grateful to Unity McDonnell for helping to organize the conference and to Guy Cowlshaw for comments on this chapter.